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Research Article

Are range limits concordant with climatic niche requirements in alien plants? Leguminous invasive plants as case study, along a latitudinal gradient, central Chile

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Abstract

How do species reach the limits of their distribution and what prevents their continued expansion beyond these ranges? Exotic plant species represent a natural experiment to answer these questions. If climate is the limiting factor, then one would expect a matching between the observed range limit for a species and the range limit predicted by its climatic niche. If there is no matching, then other factors such as dispersal limitation, competition or facilitation come into play. In this work, the predicted and observed range limits for eight exotic legume species were compared: *Acacia dealbata*, *Acacia melanoxylon*, *Cytisus striatus*, *Teline monspessulana*, *Ulex europaeus*, *Lotus corniculatus*, *Trifolium suffocatum* and *Vicia villosa*, in a latitudinal gradient in Chile. For the estimation of the observed range limit (North and South), absence/presence data were obtained from 30° to 43.1° south latitude. For the estimation of the predicted range limits, GBIF presence data were used to construct the global climatic niches, identifying suitable climatic zones (presences) and unsuitable climatic zones (absences). With this information, presence probability models were constructed with hierarchical Huisman-Olff-Fresh (HOF) regression, from which the predicted range limits (North and South) were obtained. Our results suggest that the species *Acacia dealbata* and *Cytisus striatus* have reached their predicted edge at the northern and at the southern end of the gradient. The rest of the species have not yet reached this limit across both geographic edges. At the southern end of the gradient, most species have not reached the limit predicted by the climatic niche; except for *Cytisus striatus* whose observed range limit is higher than predicted. Factors other than climate are discussed to explain the discrepancies between observed and predicted range limits.

Key words: Biogeography, climate, legumes, niche requirements, range limits

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Introduction

Charles Darwin (1957) provided the first hypothesis to understand the factors that set limits to species geographic distribution; he proposed that abiotic factors (climate) are important at the abiotic stressful limits of distribution while species biotic interactions become more important at the more benign extreme of the distribution. Nowadays, this framework plays a central role in modern biogeography (Gaston 2003; Sexton et al. 2009) and is assumed a ubiquitous

biogeographic pattern (Louthan et al. 2015). New reformulations have proposed to understand range limits of species (Ettinger and HilleRisLambers 2017; Sirén and Morelli 2020; Paquette and Hargreaves 2021), however, they maintain the basic concepts proposed by Darwin.

Hargreaves et al. (2014) proposed a hierarchical approach to understand range limits using the climatic niche of species. This framework predicts the climatic niche limits (CNL) i.e. the geographic limits predicted from climatic niche, and compares it with the range limit (RL), i.e. the observed limits in the extremes of distribution. If RL - CNL = 0, populations located at the limit range, perfectly match between climatic niche requirements and the extreme of distribution; if RL - CNL < 0, beyond RL there are suitable habitats, but they cannot be colonized by species due to dispersal limitation, introduction time or negative biotic interactions (competition, predation); if RL – CNL > 0, in RL populations are occupying unsuitable habitats, they are sink populations which must be continuously supplemented by individuals from source populations in order to persist. Another explanation is that species establish positive interactions with other species, allowing expansion due to facilitation with other plant (Badano et al. 2007; Arredondo-Núñez et al. 2009). Biological invasions provide useful insights to learn about dynamics of species range limits (Sexton et al. 2009). Given that invasive species may have colonized habitats quite different to those existing in their native ranges, we have a natural experiment to examine whether the new range limits depart from expectations from climatic requirements (Keane and Crawley 2002; Gaston 2003; Goncalves et al. 2022).

Climatic niche analysis has been prolifically used to understand the biogeography of biological invasions (Peterson 2003; Thuiller et al. 2005; Broennimann et al. 2007; Reed et al. 2008; Gallagher et al. 2010; Peña-Gómez et al. 2014; Cabra-Rivas et al. 2016). The global climatic niche enables exploration of the climatic potentialities of species using the totality of occurrences recorded for the species across invaded regions (Gallien et al. 2012; Taucare-Ríos et al. 2016). In this study, we assessed if RL is within the variation of CNL using global climatic niche. These methodologies were applied to a set of eight exotic leguminous plants species, invasive in central Chile, and in other regions of the world (Quiroz et al. 2009). Finally, we also discussed its applicability to other biogeographic situations, and to what extent the hypothesis proposed by Hargreaves et al. (2014) give us clues about the geographic dynamics of these eight species.

Methods

The setting

Central Chile concentrates an interesting vascular flora; due to its high degree of endemism and the intense deterioration of ecosystems, this region has been considered a "hotspot" of biodiversity (Armesto et al. 1998; Myers et al. 2000). The notable climatic latitudinal gradient existing in central Chile i.e, decrease of temperatures and an increase of precipitations with latitude has been largely documented in diverse studies (Di Castri and Hajek 1976; Di Castri 1991; Garreaud et al. 2009; Carretier et al. 2018), hence it constitutes an ideal scenario to conduct a natural experiment to test biogeographic hypothesis. We will use this climatic gradient to examine distribution responses of invasive species belonging to the Family Leguminosae along central Chile.

Chile has approximately 690 species of introduced plants (15% of the total flora), being 70% of them of Eurasian origin (Arroyo et al. 2000). These species are spreading into areas with native vegetation, thus affecting the composition and structure of natural communities (Pauchard and Alaback 2004; Bustamante and Simonetti 2005). Approx. 60% of human population is concentrated in central Chile. There is an intensive land use, deforestation and habitat fragmentation, all factors that are regarded as the drivers of biological invasions (Arroyo et al. 2000). During the last years, studies of plant invasion in central Chile have increased significantly (Arroyo et al. 2000; Sax 2002; Pauchard and Alaback 2004; Bustamante and Simonetti 2005; Castro et al. 2005; Peña-Gómez and Bustamante 2012; Fuentes et al. 2014; Peña-Gómez et al. 2014; Montecino et al. 2016). To date, we have a reasonable knowledge about the diversity of exotic species in Chile, however, their biogeography is quite limited (Fuentes et al. 2013, but see Peña-Gómez et al. 2014; Montecino et al. 2016). Our database about the presence of invasive plants for Chile is limited, and the estimation of range limits is only qualitative and at a very coarse spatial scale. Fuentes et al (2013) presented an update about the magnitude of plant invasion in Chile. This information, concomitantly with a local book (Fuentes et al. 2014) was used to select the eight exotic species of this study which are described ranging between 30° and 42° latitude.

Among the numerous exotic species recorded for central Chile (Fuentes et al. 2014), it was decided to work with exotic trees, shrubs, and herbs of the Family Fabaceae (Leguminoseae). These species are regarded as invasive in different parts of the world (Ndlovu et al. 2013; Richardson et al. 2015) and most of them have produced significant ecological impacts in Chile (García et al. 2014, 2015). Taxonomically, these species are well known, their distribution has been documented for central Chile and are conspicuous components of anthropogenic landscapes. The species selected for this study are *Acacia dealbata*, *Acacia melanoxylon*, *Cytisus striatus*, *Teline monspessulana*, *Ulex europaeus*, and *Lotus corniculatus* as well as two herbaceous species, *Trifolium suffocatum* and *Vicia villosa*.

Global climatic niche

Global occurrences data (presences) for the eight exotic species were downloaded during 2019 using the *occ2df* function from the *spocc* package in R (version 0.7.0), which retrieves geographic data for species from several databases as Global Biodiversity Information Facility (**GBIF**), the Atlas of Living Australia (**ALA**), Biological Information Serving Our Nation (**BISON**), EcoEngine, Integrated Digitized Biocollections (**iDigBio**), and iNaturalist (**iNat**). Occurrences were selected if they had a georeferencing error of less than 1 km. To avoid redundancy, duplicate records across databases were identified and removed during data processing (Suppl. material 1 in which we show global occurrences for species). Local occurrences were recorded from 30° to 43° south latitude (Fig. 1), using two transects, one located along the coast and the other, at the central valley. We disposed plots (2 × 50 m), placed along the verge of secondary or tertiary roads, with low management practices; roads are adequate sampling sites as they are the most obvious corridors for the spread of invasive species (Von der Lippe and Kowarik 2008; Barros and Pickering 2014; Van Der Ree et al. 2015). Each plot was located every 10 km, encompassing a total of 264 plots (132 plots per transect). We collected plant samples for further identification in the lab. From this information,

Figure 1. Graphic representation of the points sampled (red) to register the presence/absence of the eight exotic species of this study, across central Chile.

the observed Northern and Southern Range Limits (NRL and SRL respectively) was estimated, each properly georeferenced; they were obtained empirically, recording the last presence for each species at the extremes of latitudinal gradient.

For the estimation of global climatic niche, the climatic grid procedure was used (Broennimann et al. 2012). This method allows the visualization of the climatic niche in a multidimensional space, obtained from Principal Component Analysis (PCA). Specifically, this method was used by means of a data treatment in which: (i) 10000 geo-referenced random points were generated to depict the global climatic environment; (ii) 5300 geo-referenced random points were generated to depict the climatic environment in Chile, through QGIS (version 3.6.1); iii) for climatic characterization and from each of the random points, climatic variables were obtained from Worldclim 2.0, at 1 km2 resolution (Fick and Hijmans 2017), this database includes 19 climatic variables of precipitation and temperature, averaged from 1970 to 2000.The climatic grid procedure (Broennimann et al. 2012) is basically a PCA, which has the advantage of transforming a number of correlated variables into a small number of uncorrelated linear combinations of the original variables (principal components). Unlike other modeling approaches, PCA does not require pre-selecting climatic variables, as the principal components themselves could be used as predictors, reducing the dimensionality of the dataset but maintaining the same information of the original climatic variables (Sillero et al. 2021). Finally, climatic data were correlated with random points through PCA, thus generating the climatic grid (Broennimann et al. 2012). Four regions were identified in the climatic grid (multivariable climatic space): (i) global species occurrences which represent global niche; (ii) the 10.000 random points, depicting the global climatic environment; (iii) local species occurrence which represents local niche in Chile; (iv) the 5300 random points depicting the climatic environments in Chile (Fig. 2). For the purposes of this study, we focus on regions (i) and (iv). Using these two regions, we could define suitable and unsuitable climatic habitats in central Chile; suitable climatic habitats occur in the intersection between

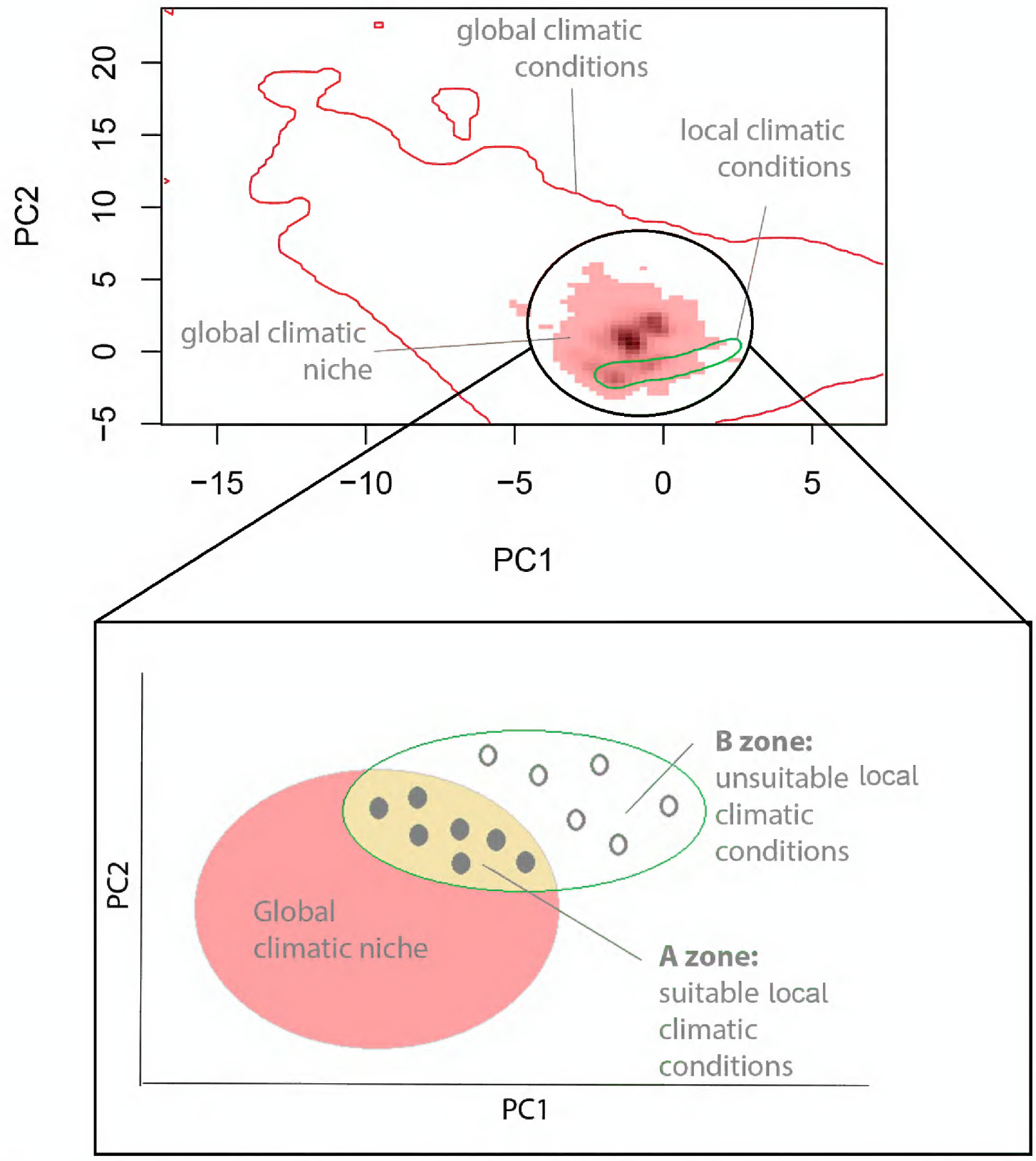

Figure 2. Graphic representation of the climatic grid and global climatic niche to identify suitable and unsuitable habitats **A** PCA with global climatic niches, intersected with the regional scale (study area in central Chile) climate niche. Pink cells: global climatic niche; green line: local climatic conditions in central Chile; red line: global climatic conditions **B** identification of suitable (black points) and unsuitable conditions (white points) for the species in the study area in Chile. Figure obtained from Goncalves et al. (2022) with permission of the authors.

the global climatic niche and the climatic environment in Chile while unsuitable climatic habitats occur in the climatic environment of Chile that is outside the global climatic niche (for more details see Fig. 2). This analysis was conducted in R with *ecospat* package and the R script is available in Suppl. material 2.

HOF curves

For zone A and B, 1325 randomly points were collected (25% of the total), thus obtaining a data vector of 1 (from zone A) and 0s (from zone B). The sampling procedure was repeated 50 times, thus obtaining for each time a data vector with 0s and 1s. Using these 50 data vectors, 50 HOF curves were generated (Oksanen and Minchin 2002). Basically, HOF curves are logistic regression models which represent species responses along environmental gradients, given a sample of suitable and unsuitable points (Fig. 2), the best model was selected using likelihood ratio tests or Akaike criteria (Ihaka and Gentleman 1996). HOF curves provide a set of parameters which

describe different curve characteristics; one of them, the Outer Border defined by the gradient value where the response curve reaches exp (-2) relative to the highest estimated response value (Heegaard 2002). The latitude at which we obtained the Outer Border was considered an estimate of CNL predicted from global climatic niche. The bootstrap analysis was conducted in R, and R script is available in Suppl. material 3.

In summary, for each species, 50 HOF curves were generated, thus estimating 50 values for the Northern and 50 values for Southern CNL. To explore the variability of the estimates, a bootstrap distribution was used for Northern and Southern CNL, with 10.000 random resampling with replacement. If the RL falls within 95% confidence interval of bootstrap distribution of northern or southern CNL, the hypothesis is that RL – NL = 0 was accepted; otherwise, it was rejected.

Results

Acacia species (*A. dealbata and A. melanoxylon*) presents the broadest latitudinal range in Chile (Table 1); *A. dealbata* was the species with a higher number of presence records in the field (Table 1). On the other hand, *Trifolium suffocatum* was the species with the lowest latitudinal range and one of the species with lowest number of presence records in the field work in Chile (Table 1).

For the northern distribution of *Acacia dealbata* and *Cytisus striatus*, a matching between the observed and predicted north range limit was detected (Table 2), while for the rest of the species the observed north range limit was significantly lower than predicted (Table 2, Figs 3, 4). For the southern distribution of *Acacia dealbata* and *Cytisus striatus*, matching between observations and predictions was founded; for *Acacia melanoxylon*, observed RL was lower than expected, and for the rest of the species, the observed southern range limit was significantly higher than predictions (Table 3).

Discussion

The geographic position of RL was quite similar between the northern and southern range; at the northern range, in only two species (*Acacia dealbata* and *Cytisus striatus*), the RL was explained by climate. For the rest of species, the RL was explained by other factors such as dispersal limitation or negative biotic interactions. At the southern range, for *Acacia dealbata* and *Cytisus striatus*, the RL matched with climatic expectations as well; in one species (*Acacia melanoxylon*), RL was explained by facilitation and for the rest of species, RL was explained by negative biotic interactions and dispersal limitation.

For *A. dealbata and C. striatus*, climate explained RL either at the northern or at the southern border. This matching may indeed be attributed to their high ornamental value and widespread cultivation in parks, gardens and road borders, with strong anthropogenic subsidies in terms of resources and conditions (Van Kleunen et al. 2018; Beaury et al. 2023). This increased human-mediated dispersal and cultivation likely enhance their chances of expansion, allowing them to reach the maximum extent of their distribution without dispersal limitation. *A. dealbata* is regarded one of the most successful exotic trees in central Chile with significant impacts on native biodiversity (Fuentes-Ramírez et al. 2011). Our results give support to this invasive success. Firstly, its niche requirements match with prevailing climatic conditions; secondly, there is no dispersal limitation; thirdly it is a strong competitor over native

plants due to allelopathic effects on the germination and growth of seed and seedlings (Aguilera et al. 2015), and a faster growth rate relative to native trees (Fuentes-Ramírez et al. 2011). However, there are some ecological constraints that can limit further expansion because it has resulted in becoming the most attacked exotic plant by herbivorous insects in invaded ranges which, in turn, can be used by biological control in different parts of the world (Wilson et al. 2011; Wilgen et al. 2023).

At the southern range, *Cytisus striatus* also matched RL with climatic niche. This result may be attributed to a low cold or freezing resistance of this species, as it has been documented in the northern hemisphere (Beans et al. 2012; Thomas and Moloney 2013; Winde et al. 2020).

Table 1. Number of local presence/absence records per species obtained from field work and global presence records obtained from different databases (see text above).

Species	Presence/absence points in central Chile				Latitudinal observed range and range size	Global presence points
	Presence coast	Absence coast	Presence valley	Absence valley		
A. dealbata	92	32	85	46	(-32, -43.1) (11.1°)	1123
A. melanoxylon	74	57	76	55	(-32, -42.9) (10.9°)	1300
C. striatus	31	100	27	104	(-33.1, -41.4) (8.3°)	731
T. monspessulana	51	80	38	93	(-32.9, -41.1) (8.2°)	245
U. europaeus	47	84	36	95	(-35.6, -43.0) (7.4°)	500
L. corniculatus	24	107	21	110	(-33.4, -43.1) (9.7°)	2079
T. suffocatum	0	131	2	129	(-34.6, -35) (0.4°)	682
V. villosa	1	130	3	128	(-32.9, -36.9) (4.0°)	1879

Table 2. Comparison between RL and CNL at the northern limit. CNL is represented by latitude values from 0.025 and 0.975 percentile (Q). For the northern limit the comparison has three possibilities: (i) RL = CNL, climate is enough to explain this limit; (ii) RL < CNL: competition and dispersal limitation explains this limit; (iii) RL > CNL: facilitation explains this limit.

Species	$Q_{0.025}$	$Q_{0.975}$	RL	RL - CNL	Hypothesis
A. dealbata	-30.37	-33.89	-32.0	RL = CNL	Climate
A. melanoxylon	-30.80	-30.92	- 32.0	RL < CNL	Competition/dispersal limitation
C. striatus	-32.18	-34.62	-33.1	RL = CNL	Climate
T. monspessulana	-31.06	-31.17	-33.1	RL < CNL	Competition/dispersal limitation
U. europaeus	-32.27	-32.40	-36.1	RL < CNL	Competition/dispersal limitation
L. corniculatus	-18.96	-19.21	-38.7	RL < CNL	Competition/dispersal limitation
T. suffocatum	-30.33	-31.76	-34.7	RL < CNL	Competition/dispersal limitation
V. villosa	-21.61	-25.60	-32.9	RL < CNL	Competition/dispersal limitation

Table 3. Comparison between CNL and RL observed at the southern limit. CNL is represented by latitude values from 0.025 and 0.975 percentile (Q). For the southern limit, the comparison has three possibilities: (i) RL = CNL: climate is enough to explain this limit; (ii) RL < CNL: facilitation explains this limit; (iii) RL > CNL: competition and dispersal limitation explain the limit.

Species	$Q_{0.025}$	$Q_{0.975}$	RL	RL - CNL	Hypothesis
A. dealbata	-43.32	-45.02	-43.1	RL = CNL	Climate
A. melanoxylon	-42.71	-42.82	-42.9	RL < CNL	Facilitation
C. striatus	-40.72	-42.29	-41.4	RL = CNL	Climate
T. monspessulana	-45.51	-45.61	-41.1	RL > CNL	Competition/dispersal limitation
U. europaeus	-49.08	-49.15	-43.0	RL > CNL	Competition/dispersal limitation
L. corniculatus	-47.60	-47.80	-43.1	RL > CNL	Competition/dispersal limitation
T. suffocatum	-38.33	-40.77	-35.0	RL > CNL	Competition/dispersal limitation
V. villosa	-53.64	-54.37	-36.9	RL > CNL	Competition/dispersal limitation

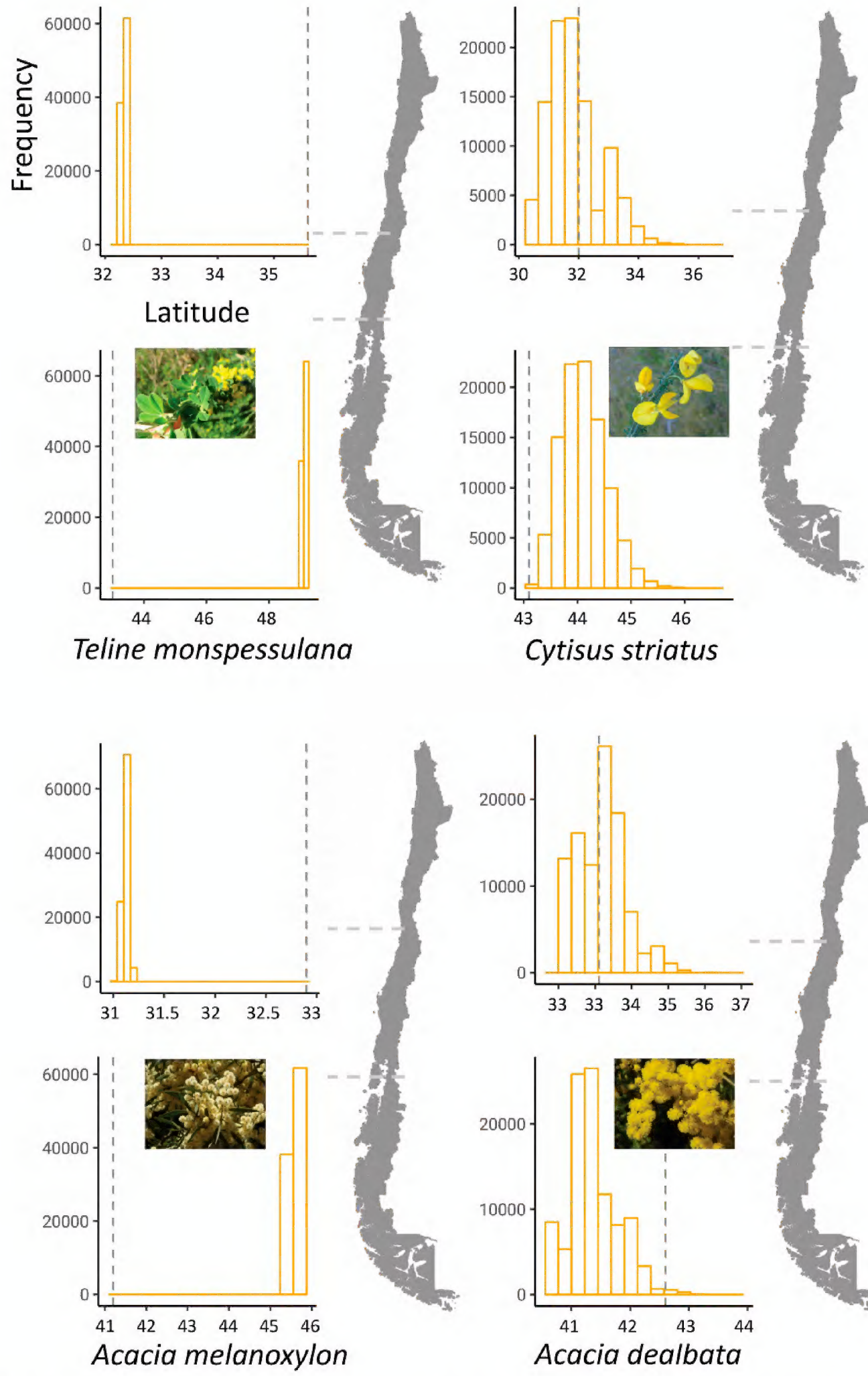

Figure 3. Bootstrap distribution of Northern and Southern CNL, obtained from global niche models, for *Teline monspessulana*, *Cytisus striatus*, *Acacia melanoxylon* and *Acacia dealbata*, central Chile.

At the northern range, the abiotic environments are relatively hostile to plant species. Under these conditions, plant-plant facilitation should be promoted, according to theory (Bertness and Callaway 1994; Lortie and Callaway 2006); however, we did not find evidence of such mechanism. We suggest that the mismatch detected between observation and expectation for six species (Table 1) can be attributed to dispersal limitations (low propagule pressure) due in part to a relatively low human settlement. The southern end of the climatic gradient in turn, hosts a high plant species diversity in Chile as well as an increase of the forest biomass (Bannister et al. 2012). This increased diversity may render these communities less invasible due to biotic resistance or competitive

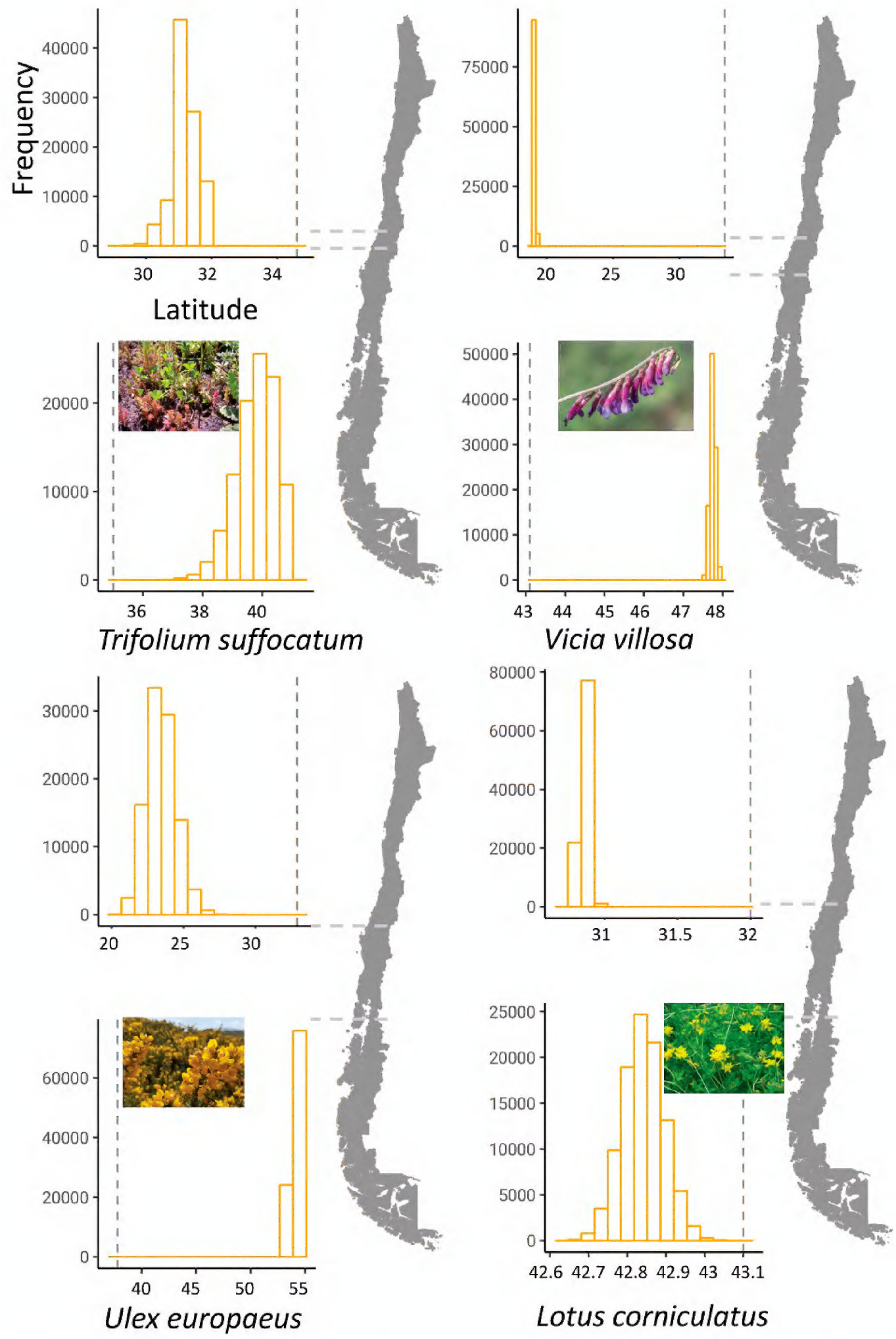

Figure 4. Bootstrap distribution of Northern and Southern CNL, obtained from global niche models, for *Trifolium suffocatum*, *Vicia villosa*, *Ulex europaeus* and *Lotus corniculatus*, central Chile.

mechanisms that limit the establishment of invasive species (Levine et al. 2004; Guo et al. 2023). Our results are consistent with Callaway's hypothesis (Bertness and Callaway 1994; Lortie and Callaway 2006), who suggests that less hostile environments, such as the southern border, may induce higher competitive pressure on exotic plants, thus resulting in constrained expansion of exotic plants further south. In summary, we propose that dispersal limitation may play an influential role at the northern border (lower latitude), while competition is more important at the southern border (higher latitude). Further field experiments are needed to test these biogeographic hypotheses.

In the southern range, *Acacia melanoxylon*, exhibited its RL beyond predictions from climatic niche. Mechanisms such as facilitation by human use, potential

nurse species interactions, or local adaptation and expansion of tolerance ranges may explain these patterns. For example, a study by Turner et al. (2015) about invasive thistle (*C. diffusa*) suggests that the physiological tolerances of *C. diffusa* may have expanded in the invaded range. Invasive species tend to present adaptive plasticity and niche expansion (Moran and Alexander 2014; Pack et al. 2022). These hypotheses warrant further investigation through transplant experiments to elucidate the underlying mechanisms driving these distribution patterns.

The study of the causal factors that explain RL along environmental gradients has proven to be a fruitful research program linking biogeography, ecology and evolution (Holt and Keitt 2005; Sexton et al. 2009; Louthan et al. 2015). Most efforts have been addressed to designing proper field experiments to discern the microevolutionary and ecological factors which are responsible for such limits (Geber 2011; Hargreaves et al. 2014; Sexton and Dickman 2016); however less effort has been devoted to inferring RL from climatic niche using statistical techniques. The method applied in this study proposes a methodology to infer statistically, the expected range limits based on climatic niche requirements; this method establishes the geographic position species range limits, so allowing us to dispose with precision where to put transplants' experiments to test biogeographic hypotheses proposed by Hargreaves et al. (2014).

Conclusion

In conclusion, our study sheds light on the interplay between observed range limits and the global climatic niche for leguminous invasive plants in central Chile. While the climate-based limitation hypothesis is partially supported, with only two species showing concordance between niche and distribution at the northern and southern edge, our findings suggest that climatic conditions alone do not fully explain distribution patterns. This discrepancy between niche and distribution is particularly notable in areas with favorable climatic conditions, such as the southern extreme of the climatic gradient. Moreover, the idiosyncratic responses of species at both ends of the gradient highlight the importance of species-specific attributes and invasion processes that may influence distribution patterns. The complex interplay between climate, human activities, and ecological factors underscores the need for further research, particularly experimental studies, to validate and elucidate the underlying mechanisms shaping invasive plant distributions in mountainous regions like central Chile. Understanding these mechanisms is crucial for effective management and mitigation strategies aimed at controlling the spread and impact of invasive species in these ecosystems.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

ROB conceptualized, EG and MD proposed the statistical design analysis, and AA data analysis; ROB, EG and MD contributed to the writing of the text.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Global Occurrence records used per species, including date and source

Authors: Ramiro O. Bustamante, Aldo Alfaro, Estefany Goncalves, Milen Duarte

Data type: xlsx

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Link: https://doi.org/10.3897/neobiota.98.136183.suppl1

Supplementary material 2

Climaticniche in R

Authors: Ramiro O. Bustamante, Aldo Alfaro, Estefany Goncalves, Milen Duarte

Data type: txt

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Supplementary material 3

HOF curves and bootstrat in R

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Data type: R file

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